

CAVE BEARS AND THEIR CLOSEST LIVING RELATIVES: A 3D GEOMETRIC MORPHOMETRICAL APPROACH TO THE FUNCTIONAL MORPHOLOGY OF THE CAVE BEAR *URSUS SPELAEUS*

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Abstract: The diet of the cave bear group (*Ursus spelaeus*) has been debated extensively. Traditionally, *U. spelaeus* was thought to be herbivorous, but more recently studies have shown that it was potentially omnivorous. Presented here is a preliminary study using three-dimensional geometric morphometrics on mandibles of *U. spelaeus* and its congeners. Multivariate analyses of variance indicate the allometric nature of sexual dimorphism. Principal component analyses and analyses of variance reveal the relationship between morphology and diet in the mandible of extant bears, displaying a gradient from carnivory to herbivory; *U. spelaeus* is found at the herbivorous extreme, supporting the hypothesis that cave bears were highly herbivorous. The position of the masseteric fossa in *U. spelaeus* indicates large bite forces necessary for the mastication of tough plant materials. *U. americanus* has a mandible shape which may reflect previous selection pressures. The necessity of correcting for allometry is shown by comparing the results for corrected and uncorrected data.

Key words: Cave bear, *Ursus spelaeus*, Ursidae, Pleistocene, mandible, masseteric fossa, 3D geometric morphometrics, allometry, functional morphology, diet

INTRODUCTION

There are eight living species of Ursidae in the world today, spread over five genera: *Ursus*, *Helarctos*, *Tremarctos*, *Ailuropoda* and *Melursus*. In the Pleistocene of Europe, however, the now extinct cave bear group (*Ursus spelaeus*) was also present. Its closest living relatives are all members of the genus *Ursus* (*U. arctos*, *U. americanus*, *U. maritimus* and *U. thibetanus*) and they are omnivorous with the exception of *U. maritimus*, which is a pure carnivore (Tab. 1). *U. spelaeus* is thought to have been primarily herbivorous (Bocherens et al., 1997; Bocherens et al., 1994; Christiansen, 2007; Stiner et al., 1998) based on the morphology of its dentition and isotopic analyses, although this interpretation is not supported universally (Figueirido et al., 2009; Richards et al., 2008).

Previous morphological and morphometrical studies have shown a strong correlation between feeding ecology and cranio-dental morphology for the family Ursidae (Christiansen, 2008; Sacco and Van Valkenburgh, 2004). Figueirido et al. (2009) have expanded on this by using 2D geometric morphometrics to make inferences on the feeding ecology of *U. spelaeus* and giant short-faced bear *Arctodus simus*. This preliminary paper builds on the

approach of Figueirido et al. (2009) by using 3D geometric morphometrics and by correcting for allometry. Furthermore, the nature of *U. spelaeus* sexual dimorphism, shape-based or size determined, will be tested.

Tab. 1. Dietary preferences of bear species (in %), based on scats. This technique underestimates the exact amounts of animal matter consumed. used to interpret the results of the morphometric analyses. The percentages do not add up to 100, as the data are calculated from averages of several unrelated studies; n represents the number of studies utilised (modified from Mattson, 1998).

taxon	n	foliage	roots	soft mast	hard mast	inverte-brates	verte-brates
<i>U. maritimus</i>	2	1	0	0	0	0	98
<i>U. americanus</i>	32	20	0	55	11	5	4
<i>U. thibetanus</i>	7	15	0	35	43	5	2
<i>U. arctos</i>	43	27	7	42	6	6	11

MATERIALS AND METHODS

To test between the proposed alternative diets for *U. spelaeus*, specimens of its congeners (*U. arctos*, *U. thibetanus*, *U. americanus* and *U. maritimus*) were examined. Other bear genera were excluded as a narrow allometry approach (Conroy, 1987) was employed here to limit the influence of phylogeny on the results. Specimens have been studied in the following museums: Museum of Natural History, London, UK; Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität, Berlin, Germany; Natural History Museum, University of Oslo, Oslo, Norway; Centre de recherches de la grotte Scladina Asbl Archéologie Andennaise, Scladina, Belgium; and the National Museum of Natural History Naturalis, Leiden, The Netherlands. A full list of all the specimens is given in the appendix.

As the mandible is part of the masticatory system and its shape is expected to hold information about diet, it is the focal element of this study. Additionally, mandibles are generally relatively well represented in recent and fossil museum collections, thus ensuring larger sample sizes. Specimens of *U. spelaeus* and its four closest living relatives were digitised with a Microscribe G2 desktop digitising system (Immersion



Fig. 1. Positions of the landmarks on a mandible of *Ursus spelaeus* from the Landesmuseum Joanneum, Graz, Austria. The landmarks are described in Tab. 1.

Corporation, San Jose, CA). Juveniles were not digitised and, wherever possible for the extant species, equal numbers of males and females were included.

When both hemimandibles were present, the more complete was chosen for digitisation. Landmarks for 3D digitisation were chosen to reflect functional aspects of the mandibular corpus (Fig. 1 and Tab. 2). In addition to standard mandibular landmarks, the masseteric fossa has also been included. The masseteric fossa is a character that is directly related to masticatory function, yet has not been analysed previously. The condyle and coronoid process were not used, because the choice of landmarks was limited by the preservation of the fossils.

Tab. 2. Landmarks used for describing mandibular shape. The landmarks are displayed in Fig. 1. Landmark types determined according to Bookstein (1991).

Landmark		Description	Reflects
1.	Type 2	Most postero-ventral point of the symphyseal region	Position and size of symphyseal region
2.	Type 2	Most postero-dorsal point of the symphyseal region	Position and size of symphyseal region
3.	Type 2	Most antero-ventral point of the masseteric fossa	Insertion, moment arm and size of several jaw muscles
4.	Type 2	Most posterior point of the alveola of M_3	Relative sizes and positions of individual dental elements
5.	Type 2	Midpoint on the rim between the lateral sides of the alveolae of M_3 and M_2	Relative sizes and positions of individual dental elements
6.	Type 3	Most ventral point on the mandibular corpus directly ventral of landmark 5	Shape of mandibular corpus
7.	Type 2	Midpoint on the rim between the lateral sides of the alveolae of M_2 and M_1	Relative sizes and positions of individual dental elements
8.	Type 2	Most dorsal point on the labial border of the alveolus of M_1	Relative sizes and positions of individual dental elements
9.	Type 3	Most ventral point on the mandibular corpus directly ventral of landmark 8	Shape of mandibular corpus

Using MorphoJ 1.01b (Klingenberg, 2008), raw 3D coordinates were scaled, rotated and translated by Procrustes superimposition; the resulting Procrustes coordinates represent shape. Shape associated with size (i.e., allometry), however, is still present in the data at this point. To remove the effects of allometry, a pooled regression analysis within species of the Procrustes coordinates onto log centroid size was performed (Bookstein, 1991; Mitteroecker et al., 2005). This analysis assumes that the allometry of the different species has the same slope, but other intercepts; it has previously been shown to give good results (Cardini and O'Higgins, 2004). Principal Component Analyses (PCA) was then conducted on the regression residuals instead of the Procrustes coordinates.

All statistical tests were performed in SPSS ver. 16.0 (SPSS Inc., Chicago, IL). After a test for homogeneity of variances, an analysis of variance (ANOVA) was performed on the PCA scores to determine the significance of species effects along each component. A multivariate analysis of variance (MANOVA) was performed on those principal components found to be significantly correlated to the variable species to determine the effects of sex. Independent samples t-tests were performed on several occasions to show whether two populations were different based on the principal component scores.

An error estimate as a percentage of intraspecific variation was calculated following Adriaens (2007), using tpsSmall (Rohlf, 2003). For this estimate, two specimens of the species *U. arctos* were each digitised three times. To compare the estimated measurement

error to the interspecific differences, the averaged landmark configuration per species was calculated in MorphoJ (Klingenberg, 2008), and the estimated measurement error was expressed as a percentage of the smallest interspecific Procrustes distance.

RESULTS

The measurement error estimate from the re-digitising exercise is 9.1% of the intraspecific variation. As this is substantially less than the smallest interspecific difference (48.4%, between *U. arctos* and *U. thibetanus*), it is unlikely to have affected the results.

A test of homogeneity of variances on the PC scores of the Procrustes coordinates shows that all variances are homogenous, except for PC5 ($\alpha < 0.01$). ANOVA shows that species effects are significant ($\alpha < 0.01$) on the first three principal components, which account for 64.0% of total variance. MANOVA on the first three principal components shows a significant sex effect ($p = 0.034$).

A test of homogeneity of variances on the regression residuals, after regressing the Procrustes coordinates onto centroid size, shows that variances are homogenous on all principal components except for PC4 ($\alpha < 0.01$). ANOVA shows that the species effects are significant on principal components 1 to 5 and 9 ($\alpha < 0.01$). The first five principal components account for 88.2% of the overall morphological variance (PC scores are displayed in the appendix) and principal component 9 accounts for an additional 1.2%. MANOVA on the first five principal components and PC9 to determine the effect of sex on the PC scores is not significant ($p = 0.336$).

The principal component analysis of residuals clearly differentiates between the species on PC1 and PC2 (Fig. 2), but gives better separation between *Ursus spelaeus* and the other ursid species on PC1 and PC3 (Fig. 3).

Principal component 1 shows a gradient from low to high scores from *Ursus spelaeus*, *U. arctos* and *U. thibetanus*, *U. americanus* to *U. maritimus* (Figs. 2 and 3). The position of

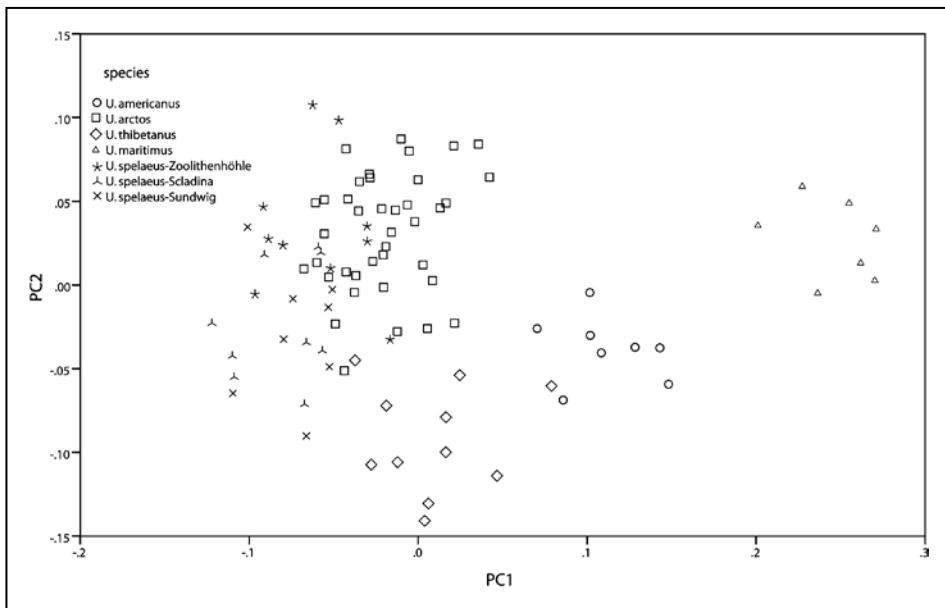


Fig. 2. Principal component analysis on the regression residuals (allometrically corrected); PC1 vs PC2. Circles: *Ursus americanus*; triangles: *U. maritimus*; squares: *U. arctos*; diamonds: *U. thibetanus*; asterix: *U. spelaeus* from Zoolithenhöhle, Germany; tripod: from *U. spelaeus* from Scladina, Belgium; cross: *U. spelaeus* from Sundwig, Germany.

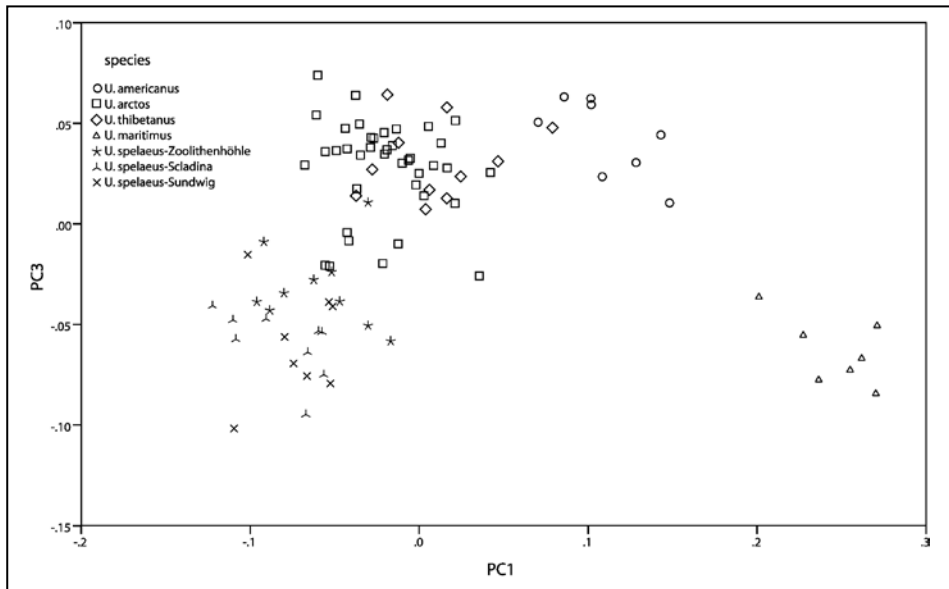


Fig. 3. Principal component analysis on the regression residuals (allometrically corrected); PC1 vs PC3. Circles: *Ursus americanus*; triangles: *U. maritimus*; squares: *U. arctos*; diamonds: *U. thibetanus*; asterisk: *U. spelaeus* from Zoolithenhöhle, Germany; tripod: from *U. spelaeus* from Scladina, Belgium; cross: *U. spelaeus* from Sundwig, Germany.

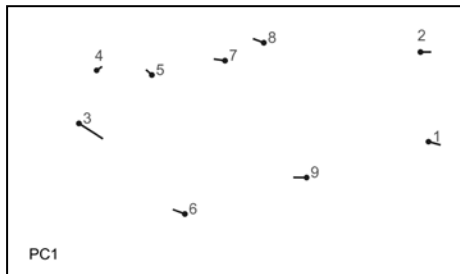


Fig. 4. Shape changes on PC1 after correction for allometry; the lines represent a change of 0.1 in positive direction on the first PC.

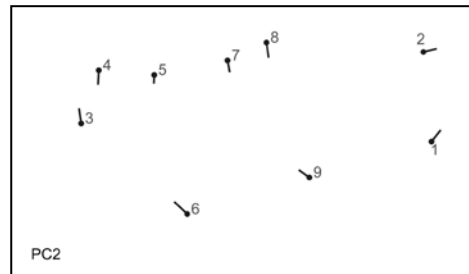


Fig. 5. Shape changes on PC2 after correction for allometry; the lines represent a change of 0.1 in positive direction on the first PC.

U. americanus does not perfectly reflect present diet, but this may be due to different selection regimes in the recent past (see Discussion below). The position of the most antero-ventral point of the masseteric fossa, mostly in ventrorostral-dorsocaudal direction, is the largest factor responsible for the shape changes along this axis (Fig. 4). The other landmarks, except landmark 4, are primarily influenced by the distance between the mandibular symphysis and the carnassial. With positive change along PC1 landmarks 1 and 2 move rostrally and landmarks 5 to 9 move caudally (Fig. 4).



Fig. 6. Shape changes on PC3 after correction for allometry, the lines represent a change of 0.1 in positive direction on the third PC.

The second principal component mainly distinguishes between *U. arctos* and *U. thibetanus* (Fig. 2). The most important shape change represented in PC2 is a dorsoventral flattening of the mandible, a longer distance between the carnassial and the mandibular symphysis and a smaller dorsoventral depth of mandibular symphysis at the caudal end (Fig. 5). Additionally, the most antero-ventral point of the masseteric fossa moves dorsally.

Principal component 3 roughly divides the data into two groups: *U. maritimus* + *U. spelaeus*, and *U. arctos* + *U. thibetanus* + *U. americanus* (Fig. 3). The position of the most antero-ventral point of the masseteric fossa, mostly in caudoventral-rostrordorsal direction, is the largest factor responsible for the shape changes along this axis (Fig. 6).

The other landmarks are associated with overall shape changes of the mandible (Fig. 6). Fig. 3 does not show any obvious differences between *U. arctos* and *U. thibetanus* on PC1 and PC3. Independent samples t-tests show, however, that they do significantly differ from each other on PC2 (Fig 2B), PC4, PC5 and PC9 ($\alpha < 0.01$).

As the results of Figueirido et al. (2009), who did not apply an allometric correction to their data, are based on all extant bear taxa, they are not directly comparable to those of the present study. To show the effects of allometry on the PCA, uncorrected Procrustes coordinates of the present *Ursus*-only sample were plotted (Fig. 7). The result shows no separation between the taxa, whereas the plots of the residuals (Figs. 2 and 3) clearly distinguish between the species examined.

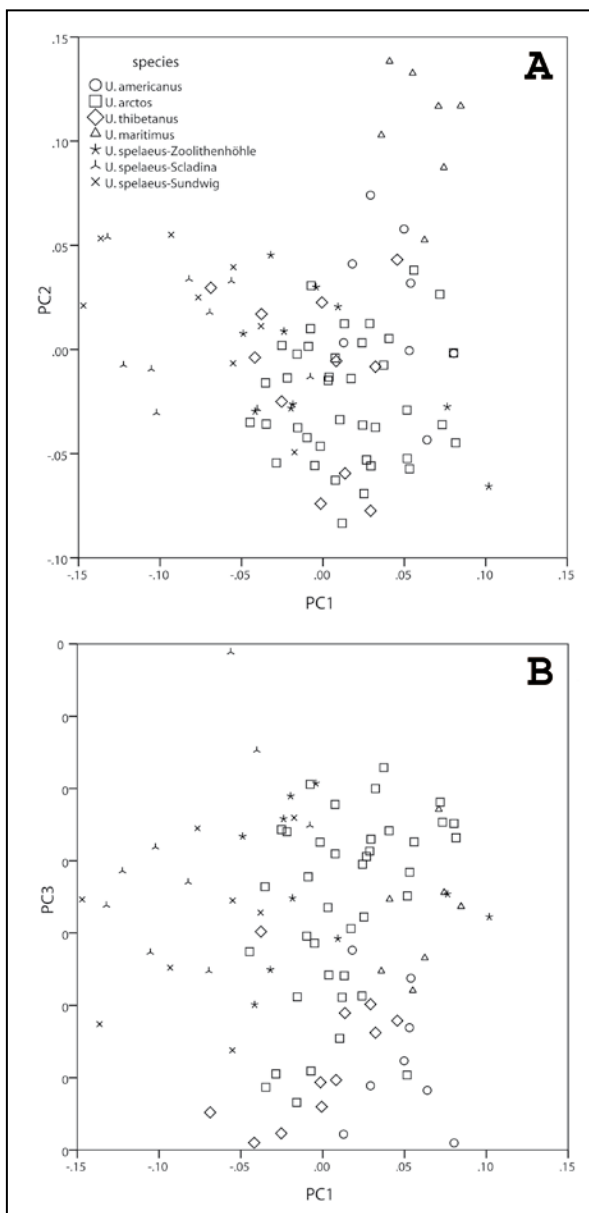


Fig. 7. Principal component analysis on the raw (allometrically uncorrected) Procrustes coordinates; A. PC1 vs PC2; B. PC1 vs PC3. Circles: *Ursus americanus*; triangles: *U. maritimus*; squares: *U. arctos*; diamonds: *U. thibetanus*; asterix: *U. spelaeus* from Zoolithenhöhle, Germany; triangle: from *U. spelaeus* from Scladina, Belgium; cross: *U. spelaeus* from Sundwig, Germany.

DISCUSSION

The outcomes of the two multivariate analyses of variance imply that sexual dimorphism in Ursidae is primarily allometric and has been filtered out effectively by regressing PC scores onto centroid size. This makes it reasonable to consider males and females as one group in further interpretations.

The position of *U. americanus* on the first principal component, intermediate between *U. maritimus*, and the *U. arctos*/*U. thibetanus* group, does not seem to fit the present diet (Tab. 1). However, an important, but often overlooked aspect of the palaeoecology of *U. americanus* is that it has evolved to compete with the now extinct *Arctodus simus* (instead of *U. arctos*, with which it is sympatric presently) until relatively recently. *U. arctos* migrated into North America during OIS 3 or 4 in the north and OIS 2 in the south (Guilday, 1968; Kurtén and Anderson, 1974), whereas *A. simus* went extinct at the end of the Pleistocene (OIS 2) (Fiedel, 2009). *A. simus* has been hypothesised to have been carnivorous, either an active hunter of large mammals or a scavenger of large carcasses (Matheus, 1995; Mattson, 1998), although more omnivorous diets have also been proposed (Figueirido et al., 2009). *U. americanus* is omnivorous at present, but prefers to eat meat and salmon whenever given the opportunity (Aguss et al., 2007). In addition, it has a relatively long and narrow lower carnassial compared to other bears, morphologically much like the carnassial of *U. maritimus* (pers. observation). As *U. americanus* prefers meat and salmon, and has suitable dentition for such a diet, and would have had access to these substances without much competition during a large part of its evolutionary history, it is likely better adapted to these food sources than to its present diet. Only after *U. arctos* migrated into North America did *U. americanus* have serious competition over small prey and salmon and it was forced to change its diet. The soft mast that constitutes a large part of the present diet of *U. americanus* (Tab. 1) is more similar in hardness and toughness to the meat and fish it was used to than to foliage or hard mast and, because of its small size, it could relatively easily climb in the trees to obtain the mast (Kuhn and Vander Wall, 2009).

Taking the palaeoecological history of *U. americanus* into account, PC1 shows a gradient from carnivory (positive PC scores) to herbivory (negative PC scores), with *U. maritimus* and *U. spelaeus* at the respective extreme ends. This is a clear indication that *U. spelaeus* (or at least the populations from Zoolithenhöhle [previously known as Gaylenreuth], Sundwig and Scladina) was as herbivorous as previously hypothesised (Bocherens et al., 1997; Bocherens et al., 1994; Christiansen, 2007; Stiner et al., 1998) and was not similar in diet to the more omnivorous *U. arctos* (Figueirido et al., 2009; Richards et al., 2008).

The position of the most rostroventral point of the masseteric fossa determines a large part of both the first and the third principal components. This landmark provides information on both the *m. zygomaticomandibularis* and the *m. masseter profundus pars posterior* (posterior part of the deep masseter).

The first principal component shows changes in the ventrorostral-dorsocaudal direction. This is approximately parallel to the direction of the *m. masseter profundus pars posterior* and is associated with its length and its moment arm. The second principal component provides information of this landmark in dorsoventral direction, and the third principal component provides information about the position of the masseteric fossa in caudoventral-rostrorodorsal direction. Change in the latter direction influences the length of the attachment area of the *masseter profundus pars posterior*. A larger attachment area implies that the muscle can induce more force on the mandible and lengthens the moment arm of the muscle. Both *U. maritimus* and *U. spelaeus* have

a relatively large attachment area for this muscle as is shown by similar PC scores on principal component 3. The presence of large muscle forces is associated with hypercarnivory in canids, but is also found in the herbivorous panda, *Ailuropoda melanoleuca* (Sacco and Van Valkenburgh, 2004). That *U. spelaeus* and *U. maritimus* both share this feature with hypercarnivorous and herbivorous carnivores explains why they have a similar morphology in this respect, even though their diets likely are so very different. A change in the general position of the masseteric fossa, and therefore the insertion of muscles, changes the orientation of the muscle fibers relative to the centric occlusion plan, the moment arms and the lengths of the muscles. For precise interpretations, however, the insertion of the muscles on the cranium and landmarks on the condyle and coronoid process of the mandible should also be considered, as is intended for future, more elaborate, studies.

In addition to the position of the masseteric fossa, the first and second principal components also provide information on the distance between the mandibular symphysis and the carnassial, and PC2 indicates the dorsoventral depth of the mandibular symphysis at the caudal end. A shorter distance between the mandibular symphysis and the carnassial and a deeper mandibular symphysis make the mandible more resistant against bending forces when only one of the carnassials is used at one time. The distance is generally shorter in the case of more herbivorous species (Fig. 2), where the distal part of the carnassial, the talonid, is used for grinding.

The second principal component displays the relative thickness of the mandible. *U. arctos* has a relatively flatter mandible and smaller mandibular symphysis than *U. thibetanus*. *U. thibetanus* eats more hard mast than *U. arctos* (Tab. 1), which explains this difference in morphology, as hard mast requires a stronger mandible to be masticated.

The present study represents a significant methodological advance in the study of cave bear functional morphology. Figueirido et al.'s (2009) study of the functional morphology of cave bear mandibles (using a slightly different methodology and including all extant species of bears) was probably influenced by phylogeny, explaining the position of *Tremarctos ornatus* with the omnivores instead of with *Ailuropoda melanoleuca*. Furthermore, they use 2D data taken from photographs instead of 3D data. Even though hemi-mandibles are rather flat, the use of photographs renders it impossible to use landmarks on both the lingual and the labial side of the mandible in the same analysis. Thus, three-dimensional data increases the precision of the data and makes it possible to include all possible landmarks on the mandible, not just those that happen to be visible on the photograph.

In addition, allometrically corrected data yield much better separation between the groups when performing principal component analyses. This may explain the lack of separation between species in the results of Figueirido et al. (2009).

CONCLUSIONS

If a large size range is involved, correcting for allometry, can substantially improve separation between species in principal components analysis. An adequate way of doing this is by regressing Procrustes coordinates onto centroid size.

Principal component analysis on the regression residuals, after regressing Procrustes coordinates onto centroid size, is able to differentiate between the different species of the genus *Ursus*; *U. maritimus*, *U. americanus*, *U. arctos*, *U. thibetanus*, and *U. spelaeus*. The best separation between *U. spelaeus* and the other species occurs on principal components 1 and 3. Principal component 1 is associated with diet and shows a gradient for extant bears from relatively omnivorous species to relatively carnivorous species, and suggests a largely herbivorous diet for the extinct *U. spelaeus*.

The size and position of the masseteric fossa, which has not been used in geometric morphometric studies of cave bear mandibles until now, has proven to be an important aspect of mandibular functional morphology. The masseteric fossa in cave bears, as compared to modern members of the genus *Ursus*, is located relatively dorso-posteriorly. This position of the masseteric fossa gives the jaw muscles more power, which may be associated with the consumption of tough plant materials.

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GROTTENBEREN EN HUN NAUWSTE VERWANTEN: EEN 3D GEOMETRISCHE MORFOMETRISCHE BENADERING VAN DE FUNCTIONELE MORFOLOGIE VAN DE GROTTENBEER *URSUS SPELAEUS*

Samenvatting

Over het algemeen wordt aangenomen dat *U. Spelaeus* een relatief grote plantaardige component in zijn dieet had in vergelijking met zijn naaste verwanten, allen leden van het genus *Ursus*: te weten *U. arctos*, *U. americanus*, *U. thibetanus*, en *U. maritimus*. Recente studies wijzen er echter op dat *U. spelaeus* mogelijkwerwijs dezelfde mate van omnivorie ten toon heeft gespreid als *U. arctos*. Om meer inzicht in het dieet van *U. spelaeus* te krijgen, zijn bij deze voorlopige studie onderkaken van *U. spelaeus* vergeleken met die van zijn nauwste verwanten door middel van driedimensionale geometrische morfometrie.

Principale componenten analyses (PCA) zijn uitgevoerd op zowel de Procrustes coördinaten als de regressie-residuen van de regressie-analyse op de Procrustes coördinaten op centroid grootte (CS). Variantie-analyse (ANOVA) van zowel allometrisch ongecorrigeerde als gecorrigeerde PC scores wijst uit dat de eerste drie principale componenten, en de eerste vijf en negende principale componenten, respectievelijk, significant gecorreleerd zijn met soort ($\alpha < 0.01$). Dit betekent dat de resultaten inzichtelijker worden wanneer er voor allometrie gecorrigeerd wordt. Multivariate variantie-analyses (MANOVA) van de significante principale componenten zijn uitgevoerd op zowel de gecorrigeerde als de ongecorrigeerde data om de invloed van geslacht op de vorm van de onderkaak te bepalen. Het effect van geslacht op de significant soort-gecorrigeerde principale componenten resulteert in $p=0.034$ voor ongecorrigeerde data en $p=0.336$ voor gecorrigeerde data. Dit wijst erop dat seksueel dimorfisme binnen het genus *Ursus* voornamelijk allometrisch van aard is, en effectief uitgefilterd kan worden door de Procrustes coördinaten op CS te regresseren.

PC1 laat een gradiënt zien van *U. spelaeus*, via *U. arctos* en *U. thibetanus*, *U. americanus*, naar *U. maritimus*. Met inachtnaam van het gegeven dat *U. americanus* in de periode voordat *U. arctos* aan het einde van de laatste ijstijd naar Noord-Amerika migreerde, een grotere dierlijke component in zijn dieet kende, toont deze principale component een gradiënt van recente soorten met een relatief herbivoor dieet tot soorten met een relatief carnivoor dieet. *U. spelaeus* bevindt zich aan het herbivore uiteinde van dit spectrum, waardoor geconcludeerd kan worden dat *U. spelaeus* meer plantaardig materiaal heeft gegeten dan de alleseters *U. arctos* en *U. thibetanus*. Morfologisch gezien is deze principale component voornamelijk gerelateerd aan de relatieve positie van de masseterische fossa in ventrorostrale-dorsocaudale richting, maar in mindere mate ook aan de afstand tussen de mandibulaire symfyse en de knipkies. Deze twee kenmerken zijn respectievelijk gerelateerd aan de lengte en de arm van de *m. masseter profundus pars posterior*, en de stevigheid van de onderkaak ten opzichte van de kauwkracht van de kauwspieren.

PC2 maakt voornamelijk onderscheid tussen *U. arctos* en *U. thibetanus*. Morfologisch gezien geeft deze principale component voornamelijk informatie over de dorsoventrale diepte van de onderkaak, alsook over de daarmee verbonden dorsoventrale positie van de masseterische fossa. *U. arctos* heeft een relatief minder diepe onderkaak dan *U. thibetanus*, hetgeen mogelijk verklaard kan worden door het feit dat *U. thibetanus* grote hoeveelheden harde mast verorbert, waarvoor een robuuste onderkaak noodzakelijk is.

PC3 maakt onderscheid tussen *U. spelaeus* en *U. maritimus* enerzijds, en de overige berensoorten anderzijds. Het dominante morfologische aspect van deze principale component is de positie van de masseterische fossa in caudoventrale-rostrodorsale richting; bij *U. spelaeus* en *U. maritimus* bevindt de masseterische fossa zich relatief rostrodorsaal, wat zowel bij hypercarnivore hondachtigen als de planteneter *Ailuropoda melanoleuca* gerelateerd is aan grote bijtkracht.

Op basis van de gepresenteerde resultaten kan geconcludeerd worden dat *U. spelaeus* inderdaad een planteneter was, zoals voorheen al werd aangenomen, en voornamelijk vezelig materiaal gegeten heeft.

MEDVEDE JASKYNNÉ A ICH NAJBLIŽŠÍ ŽIJÚCI PRÍBUZNÍ: 3D GEOMETRICKÝ MORFOMETRICKÝ PRÍSTUP K RIEŠENIU FUNKČNEJ MORFOLÓGIE MEDVEĎA JASKYNNÉHO *URSUS SPELAEUS*

Zhrnutie

O druhu *Ursus spelaeus* (medveď jaskynný) sa bežne predpokladá, že bol pomerne viac rastlinožravý v porovnaní s jeho príbuznými, zástupcami rodu *Ursus*: *U. arctos* (medveď hnedý), *U. americanus* (medveď baribal), *U. thibetanus* (medveď ušatý) a *U. maritimus* (medveď biely). Posledné štúdie však poukazujú, že *U. spelaeus* mohol byť rovnako všežravý ako *U. arctos*. Predložená práca sa snaží vniesť viac svetla do danej témy porovnaním sánok druhu *U. spelaeus* so sánkami jeho najbližších žijúcich príbuzných použitím trojrozmernej geometrickej morfometrie.

Analýza hlavných komponentov (Principal component analyses, PCA) sa použila na Procrustove koordináty a regresné rezidua, podľa regresie Procrustových koordinát do centroidnej veľkosti (centroid size, CS). Analýza rozdielov na alometricky neupravené aj upravené PC pomery poukazuje na prvé tri hlavné komponenty, resp. na prvých päť a deväť hlavných komponentov. Tie sú významne korelované s druhom ($\alpha < 0.01$). To poukazuje, že úprava pre alometriu vylepšuje výsledky vo veľkom rozsahu.

Multivariačná analýza rozdielu významných hlavných komponentov sa použila ako na neupravené, tak aj upravené údaje v snahe určiť vplyv pohlavia na morfológiu sánky. Efekt pohlavia na hlavné komponenty, ktoré sa vzťahujú na druh pre alometricky neupravené údaje, má hodnotu $p=0.034$, zatiaľ čo pre alometricky upravené údaje je hodnota $p=0.663$. To poukazuje, že sexuálny dimorfizmus v rámci rodu *Ursus* je predovšetkým alometrický a je efektívne prefiltrovaný regresiou Procrustových koordinát do CS.

PC1 vykazuje nárast od druhov *U. spelaeus*, *U. arctos*, *U. thibetanus* a *U. americanus* k druhu *U. maritimus*. Za predpokladu, že *U. americanus* mohol byť oveľa viac mäsožravý pred imigráciou *U. arctos* do Severnej Ameriky na konci posledného zaľadnenia, toto PC vykazuje nárast od dosiaľ žijúcich zvierat s pomerne rastlinnou potravou k zvieratám s pomerne viac zástupným mäsom v strave. *U. spelaeus* je na samom konci herbivorie (rastlinožravosti) tohto spektra a preto je považovaný za viac rastlinožravého ako všežravý *U. arctos* a *U. thibetanus*. Morfologicky, toto PC je najmä spojené s pomernou pozíciou žuvačovej jamy (*fossa masseterica*) vo ventrorostrálnom-dorzokaudálnom smere, ale tiež so vzdialenosťou medzi oblasťou spojenia vetiev sánky (*symphysis mandibularis*) a trhákom. Tieto znaky môžu byť spojené s dĺžkou a momentom natiahnutia žuvacích svalov *m. masseter profundus pars posterior* a odolnosťou sánky voči sile prežúvania (resp. zhryzu).

PC2 primárne rozlišuje medzi *U. arctos* a *U. thibetanus*. Morfologicky, toto PC je najmä spojené s dorzoventrálnym rozmerom (výškou) sánky, ako aj s dorzoventrálnou pozíciou žuvačovej jamy. *U. arctos* má pomerne šithlejšiu sánku ako *U. thibetanus*, čo je možné vysvetliť faktom, že *U. thibetanus* požíra veľké množstvo tvrdého dreva, k čomu je potrebná robustná sánka.

PC3 poukazuje na rozdiel medzi *U. spelaeus* a *U. maritimus* a ďalšími druhmi medveďov. Najvýznamnejším morfológickým aspektom, vplývajúcim na tento hlavný komponent, je pozícia žuvačovej jamy v kaudoventrálno-rostrodorzálnom smere; *U. spelaeus* a *U. maritimus* majú žuvačovú jamu situovanú viac v rostrodorzálnej pozícii, čo je spojené s veľkou silou zhryzu. To sa vyskytuje ako u hyperkarnívorných psovitéch šeliem, tak aj u raslinožravej pandy veľkej (*Ailuropoda melanoleuca*).

Záverom je možné prehlásiť, že analýza hlavných komponentov potvrdila tradičný pohľad na *U. spelaeus* ako rastlinožravý druh, požívajúci tiež vláknité drevo.

Appendix

specimen ID	museum ¹	Species ²	sex ³	geographic origin	PC1	PC2	PC3	PC4	PC5
BM(NH)1961.1285	NHM	Uam	m	N.W. North America	.143	-.038	.044	-.029	.034
BM(NH)1961.1286	NHM	Uam	m	N.W. North America	.086	-.069	.063	-.034	.004
BM(NH)1961.1287	NHM	Uam	m	N.W. North America	.108	-.041	.023	-.022	.040
BM(NH)1976.197	NHM	Uam	u	N.W. North America	.148	-.059	.010	-.013	.018
BM(NH)2002.124	NHM	Uam	u	S.E. North America	.070	-.026	.051	-.040	-.008
BM(NH)1942.78	NHM	Uam	m	Canada	.102	-.005	.062	-.089	.049
BM(NH)1942.79	NHM	Uam	u	Canada	.102	-.030	.059	-.023	.060
BM(NH)1912.5.15.2	NHM	Uam	u	North America	.128	-.037	.030	-.020	.003
BM(NH)1931.6.1.1	NHM	Uar	f	S.W. Asia	-.010	.087	.030	.008	.002
BM(NH)1887.12.22.1	NHM	Uar	f	S.W. Asia	.021	.083	.010	-.025	.035
BM(NH)GERM 1010g	NHM	Uar	m	S.W. Asia	-.012	-.028	-.010	-.013	-.022
BM(NH)1852.3.2.2	NHM	Uar	u	S.W. Asia	-.021	-.001	.035	-.006	.030
BM(NH)31.2.2.1	NHM	Uar	f	Centr. Asia	.005	-.026	.048	.041	.010
BM(NH)32.12.15.1	NHM	Uar	f	Centr. Asia	-.042	.051	-.008	.000	.008
BM(NH)1942.81	NHM	Uar	f	Centr. Asia	-.044	-.051	.047	.016	.022
BM(NH)1887.5.5.3	NHM	Uar	f	Centr. Asia	-.060	.013	.074	.007	.012
BM(NH)1892.10.9.1	NHM	Uar	f	Centr. Asia	-.029	.066	.038	.030	-.012
BM(NH)1931.1.6.3	NHM	Uar	m	Centr. Asia	-.043	.008	.037	.049	.004
BM(NH)1932.5.6.1	NHM	Uar	m	Centr. Asia	-.049	-.023	.036	-.014	.024
BM(NH)1932.7.6.8	NHM	Uar	m	Centr. Asia	-.038	-.004	.064	.016	-.001
BM(NH)1856.9.22.21	NHM	Uar	m	Centr. Asia	-.061	.049	.054	.013	.021
BM(NH)1887.5.5.2	NHM	Uar	m	Centr. Asia	-.035	.044	.050	.031	.002
BM(NH)1929.5.24.1	NHM	Uar	f	N. Asia & E. Europe	-.056	.051	.036	.010	-.039
BM(NH)1888.2.20.16	NHM	Uar	f	N. Asia & E. Europe	-.022	.046	-.020	-.019	-.007
BM(NH)1888.2.20.18	NHM	Uar	f	N. Asia & E. Europe	-.043	.081	-.004	-.012	.006
BM(NH)1890.8.1.3	NHM	Uar	f	N. Asia & E. Europe	-.005	.080	.033	.002	-.024
BM(NH)1991.216	NHM	Uar	f	N. Asia & E. Europe	.036	.084	-.026	.020	.009
BM(NH)1919.7.7.3609	NHM	Uar	m	N. Asia & E. Europe	.013	.046	.040	.022	-.001
BM(NH)1919.7.7.3610	NHM	Uar	m	N. Asia & E. Europe	-.068	.010	.029	.028	-.009

BM(NH)1888.2.20.14	NHM	Uar	m	N. Asia & E. Europe	-.006	.048	.032	-.014	-.025
BM(NH)1888.2.20.15	NHM	Uar	m	N. Asia & E. Europe	-.056	.031	-.021	.018	-.023
BM(NH)1991.217	NHM	Uar	m	N. Asia & E. Europe	-.016	.031	.039	.032	-.016
MZUF-11884	Specola	Uar	f	W. Europe	.003	.012	.014	-.014	.019
ZMUO-81-57	ZMUO	Uar	m	W. Europe	.009	.003	.029	.065	-.003
ZMUO-129-58	ZMUO	Uar	m	W. Europe	-.028	.064	.043	.022	-.025
ZMUO-348-49	ZMUO	Uar	m	W. Europe	-.019	.023	.037	.000	-.013
ZMUO-3427	ZMUO	Uar	m	W. Europe	-.014	.045	.047	.017	.006
ZMUO-11847	ZMUO	Uar	m	W. Europe	-.027	.014	.043	.057	-.028
MZUF-11883	Specola	Uar	m	W. Europe	.042	.064	.026	-.023	.038
ZMUO-247	ZMUO	Uar	u	W. Europe	.021	-.023	.051	.009	.010
MZUF-3583	Specola	Uar	u	W. Europe	-.053	.005	-.021	.009	-.026
MZUF-3584	Specola	Uar	u	W. Europe	-.037	.006	.017	.048	.018
ZMUO-7376	ZMUO	Uar	u	W. Europe	-.035	.062	.034	.017	.013
ZMUO-7377	ZMUO	Uar	u	W. Europe	.017	.049	.028	.027	-.017
ZMUO-7379	ZMUO	Uar	u	W. Europe	.000	.063	.025	.044	.001
BM(NH)1878.6.18.1	NHM	Uar	u	N.W. North America	-.002	.038	.019	-.023	-.028
ZMUO-7384	ZMUO	Uar	u	Norway	-.021	.018	.045	.063	-.006
BMNH-1844.12.17.3 ^a	NHM	Uth	u	Unknown	.079	-.060	.048	.005	.019
BM(NH)1930.3.1.2	NHM	Uth	f	Centr. Asia	-.037	-.045	.014	-.021	-.007
BM(NH)1930.5.21.1	NHM	Uth	f	Centr. Asia	-.019	-.072	.064	-.009	-.014
BM(NH)1931.9.21.2	NHM	Uth	f	Centr. Asia	.047	-.114	.031	.003	-.014
BM(NH)1895.2.21.6	NHM	Uth	f	Centr. Asia	.016	-.079	.058	-.053	-.003
BM(NH)1926.10.8.41	NHM	Uth	m	Centr. Asia	.016	-.100	.013	.028	-.011
BM(NH)1927.2.7.4	NHM	Uth	m	Centr. Asia	.025	-.054	.024	-.034	-.024
BM(NH)1933.2.4.3	NHM	Uth	m	Centr. Asia	-.012	-.106	.040	-.010	-.017
BM(NH)1895.2.21.5	NHM	Uth	m	Centr. Asia	.006	-.130	.017	.004	-.074
BM(NH)1926.10.8.42	NHM	Uth	u	Centr. Asia	.004	-.141	.007	-.010	-.026
BM(NH)1880.3.20.30	NHM	Uth	u	Centr. Asia	-.028	-.107	.027	.016	-.043
BM(NH)1941.1.12.7 ^b	NHM	Uma	f	Polar region	.271	.033	-.051	.013	-.003
ZMUO-370-65-62	ZMUO	Uma	f	Polar region	.236	-.005	-.078	.025	-.032
ZMUO-370-65-68	ZMUO	Uma	f	Polar region	.270	.003	-.084	.017	-.031
BM(NH)1929.7.24.1	NHM	Uma	u	Polar region	.227	.059	-.055	.002	-.006
BM(NH)1929.7.24.3	NHM	Uma	u	Polar region	.255	.049	-.073	.032	.005
BM(NH)1929.7.24.6	NHM	Uma	u	Polar region	.262	.013	-.067	.018	.006
BM(NH)1845.12.29.8	NHM	Uma	u	Polar region	.201	.035	-.036	-.001	-.012
SC86-21-4630	Scladina	Usp	u	Scladina	-.059	.022	-.053	.021	-.008
SC82-81-3129	Scladina	Usp	u	Scladina	-.067	-.034	-.064	-.013	-.034
SC83-109-2274	Scladina	Usp	u	Scladina	-.057	-.039	-.075	.016	.004
SC83-446-3127	Scladina	Usp	u	Scladina	-.109	-.055	-.057	.049	.023

SC86-108-1478	Scladina	Usp	u	Scladina	-.110	-.042	-.048	-.002	.007
SC91-615-1475	Scladina	Usp	u	Scladina	-.091	.018	-.047	.053	-.015
SC83-436-101	Scladina	Usp	u	Scladina	-.067	-.071	-.095	.029	.035
SC87-90-40	Scladina	Usp	u	Scladina	-.058	.019	-.054	.042	.074
SC98-325-147	Scladina	Usp	u	Scladina	-.122	-.023	-.041	.019	.023
MB.Ma.2306	Humboldt	Usp	u	Sundwig	-.053	-.049	-.079	-.036	.018
MB.Ma.2311	Humboldt	Usp	u	Sundwig	-.053	-.013	-.039	-.021	.021
MB.Ma.2313	Humboldt	Usp	u	Sundwig	-.067	-.090	-.076	.023	.008
MB.Ma.2316	Humboldt	Usp	u	Sundwig	-.080	-.032	-.056	-.063	.042
MB.Ma.3029	Humboldt	Usp	u	Sundwig	-.051	-.002	-.041	-.035	-.007
MB.Ma.50659	Humboldt	Usp	u	Sundwig	-.101	.035	-.015	-.027	.010
St.445532	Naturalis	Usp	u	Sundwig	-.110	-.064	-.102	.018	.013
St.18444u	Naturalis	Usp	u	Sundwig	-.074	-.008	-.069	.019	-.002
MB.Ma.2280	Humboldt	Usp	u	Zoolithenhöhle	-.097	-.005	-.039	-.043	-.055
MB.Ma.2000	Humboldt	Usp	u	Zoolithenhöhle	-.089	.027	-.043	-.047	.019
MB.Ma.2250	Humboldt	Usp	u	Zoolithenhöhle	-.030	.026	.011	-.052	-.028
MB.Ma.2269	Humboldt	Usp	u	Zoolithenhöhle	-.047	.099	-.039	-.071	-.011
MB.Ma.2271	Humboldt	Usp	u	Zoolithenhöhle	-.092	.047	-.009	-.016	.030
MB.Ma.2279	Humboldt	Usp	u	Zoolithenhöhle	-.080	.024	-.034	-.043	.021
MB.Ma.2281	Humboldt	Usp	u	Zoolithenhöhle	-.030	.035	-.050	-.013	.007
MB.Ma.2284	Humboldt	Usp	u	Zoolithenhöhle	-.063	.107	-.028	-.100	-.080
MB.Ma.2291	Humboldt	Usp	u	Zoolithenhöhle	-.052	.009	-.024	-.023	.005
BMNH-10840	NHM	Usp	u	Zoolithenhöhle	-.017	-.033	-.058	.008	.004

(Endnotes)

- Abbreviations for the museums are used as follows: NHM: Museum of Natural History, London, UK; Humboldt: Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität, Berlin, Germany; ZMUO: Natural History Museum, University of Oslo, Oslo, Norway; Scladina: Centre de recherches de la grotte Scladina Asbl Archéologie Andennaise, Scladina, Belgium; Naturalis: National Museum of Natural History Naturalis, Leiden, The Netherlands.
 - Abbreviations for species are used as follows: Uam: *Ursus americanus*; Uar: *U. arctos*; Uth: *U. thibetanus*; Uma: *U. maritimus*; Usp: *U. spelaeus*.
 - Abbreviations for sex are used as follows: f: female; m: male; u: unsexed.
- ^a also registered in Gray's Early Register of Mammalia as BM(NH) GERM 219g
- ^b also registered in Gray's Early Register of Mammalia as BM(NH) GERM 221d

Note of authors

Late in the review process for this paper, it was announced that there is a bug in MorphoJ 1.01 (used for the analyses herein). Preliminary reanalysis indicates that the results reported here were affected by the programming error. Therefore, the results and discussions concerning PC1 and PC3 should be regarded as indicative only. As these proceedings are meant to reflect the presentations given during the symposium, the authors felt it would be appropriate to include the results as they were presented; complete reanalysis will be deferred to future publications.